

MOVEMENTS OF THE THORAX AND POTENTIAL CHANGES IN THE THORACIC MUSCLES OF INSECTS DURING FLIGHT¹

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The wingbeat frequency of insects ranges from 5 per second in some butterflies up to 1000 per second in certain midges (Sotavalta, 1947). The most carefully investigated flight performance is that of *Drosophila*, which is capable of continuous flights of up to two hours at an initial wingbeat frequency as high as 300 per second which drops to not less than 100 per second as fatigue terminates the flight (Williams, Barnes and Sawyer, 1943). This prodigious motor performance poses many questions regarding the metabolic fuel (Chadwick, 1947; Wigglesworth, 1949) and power output (Chadwick and Williams, 1949), and also demands a muscular mechanism capable of a cycle of excitation, contraction, and relaxation within an interval of three milliseconds.

In a recent study of excitation of the wing muscles of another fly, *Calliphora*, Pringle (1949) recorded a sequence of spike potentials during flight from electrodes inserted among the indirect flight muscles. Although similar in form and duration to muscle potentials recorded from other arthropods, these spike potentials showed a complete lack of synchrony with the wing movements, recurring in a rhythm of their own of one spike to every dozen or so wingbeats. Pringle concludes that each spike is the sign of the arrival of a motor nerve impulse whose action is to render the indirect flight muscles susceptible to the stimulus of stretch. Contraction of the vertical muscles stretches the horizontal muscles, and the myogenic oscillation thus established continues for as long as the requisite state of excitation is maintained by the arrival of motor nerve impulses.

This novel mechanism is in contrast to the situation encountered in a much less specialized insect, the roach *Periplaneta americana*. Excitation of muscles in the leg (Pringle, 1939) and thorax of this insect (Roeder and Weiant, 1950) is indicated by the appearance of a spike potential preceding each contraction. Although the loading of the muscle was not controlled, Roeder and Weiant recorded a latency of 3.0 milliseconds, duration of muscle potential of 4-5 milliseconds, and contraction-relaxation time of 20-25 milliseconds. Since the wing beat frequency of the roach is only 20-30 per second at room temperature, there is plenty of leeway for this relatively conventional neuromuscular system to move the wings during flight.

Measurement of wing beat frequency and muscle potentials in several insects was undertaken in an attempt to correlate these contrasting observations, and to find out more, if possible, regarding the novel mechanism described by Pringle.

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METHOD

The insect was narcotized with carbon dioxide and two small holes were made in the thoracic tergum. A glass stylus bearing two fine electrodes of 36 gauge platinum wire was cemented to the tergum with paraffin wax, in such a way that the electrode tips passed through the holes to lie among the thoracic muscles (Fig. 1). The stylus was placed in the needle holder of a crystal phonograph pick-up which was connected to the input of a conventional biological amplifier through 10 megohms. The electrodes were connected to another amplifier through loops or mercury cups. The movements of the thorax and the potentials occurring within were recorded simultaneously on a double-beam cathode-ray oscillograph.

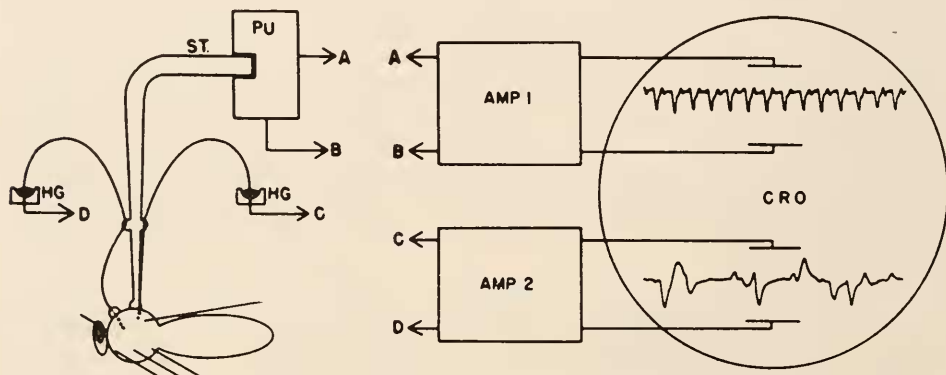


FIGURE 1. Apparatus used to make simultaneous records of thoracic movements and spikes during stationary flight. Platinum electrodes are fused to a glass stylus (ST) and make contact (CD) through mercury cups (HG) with amplifier. The stylus is inserted in a crystal phonograph pick-up (PU) which is connected (AB) with another amplifier. Removable platform below tarsi is not shown.

Stationary flight was initiated by the removal of a platform upon which the insect stood, and was maintained in some cases by a stream of air directed towards the head of the insect.

THORACIC MOVEMENTS AND POTENTIALS DURING STATIONARY FLIGHT

Periplaneta. Male roaches flew well at temperatures above 22° C. The wing-beat frequency lay between 25 and 30 per second. The relation of muscle spikes to wing movements was about as expected on the basis of the muscle studies. In records (Fig. 2 C) made with electrodes in various groups of thoracic muscles, a compound spike potential recurred at the same frequency and in fixed phase with the cycles of thoracic movement during flight. The record of the latter is quite complex, showing many harmonics, although the fundamental frequency was found to correspond with the cycle of wing elevation and depression, by viewing the insects simultaneously with stroboscopic light.

Agrotis. Several specimens of this moth were flown in the same manner. This insect showed slightly higher wingbeat frequencies (35 to 40 per second at room temperature) although the spike potential recorded from thoracic electrodes maintained the same 1 : 1 relation with the cycle of wing movement (Fig. 2 A).

At the onset of flight, the first spike was always followed by a movement, and during steady flight the spike appeared to be compounded of activity in several units. The spontaneous termination of flight took the form of a series of stepwise decreases in the amplitude of thoracic movement, accompanied by corresponding stepwise decreases in the height of the spike potential.

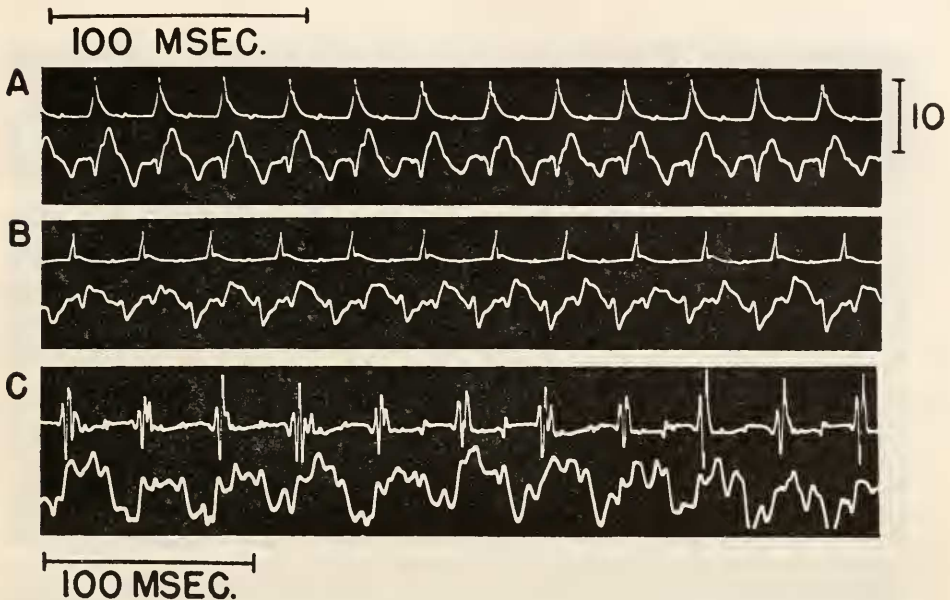


FIGURE 2. Spike potentials (upper trace) and thoracic movements (lower trace) in *Agrotis* with wings (A) and without wings (B), and *Periplaneta* with wings (C). Upper horizontal calibration applies to A and B, and lower to C. Vertical calibration, 10 millivolts.

Diptera. Flies belonging to the genera *Calliphora*, *Lucilia*, and *Eristalis* were flown in the same manner. The pattern of activity at the onset of flight is shown in Figure 3 A. The initial downward deflection is caused by the downward movement of the fly as the platform descends under its tarsi. The oscillation in the valley which follows indicates the moment when the tarsi lose their grip, following which the fly is flicked upward by the elasticity of the stylus. Flight begins about 60 milliseconds (flight reaction time) after contact with the platform is lost, and takes the form of a complex thoracic oscillation of steadily increasing amplitude (see also Fig. 3 D). No attempt has been made to analyze the pattern of thoracic movement during flight, although several characteristics may be noted: a) a fundamental frequency which corresponds with the frequency of wingbeat (this was checked by simultaneous stroboscopic observation); b) several harmonics, possibly produced by abrupt development of tension in different groups of flight muscles; 3) complex changes in the harmonic content and amplitude of the fundamental wave, which were particularly noticeable in *Calliphora* and *Lucilia*, and may be related to the characteristically erratic free flight of these insects. In *Eristalis* (Fig. 3 D), thoracic movement shows fewer fluctuations. The pattern of thoracic movement in these flies is very similar to the oscillogram

of the sound produced by *Drosophila* during flight (Williams and Galambos, 1950), and further harmonic analysis of both sound and movement patterns along the lines indicated by these authors would be of value.

In contrast to these changes in wave form and amplitude, the frequency of thoracic movement remains fairly constant in individual insects at constant temperature. Many of the insects would take only short flights, ceasing activity

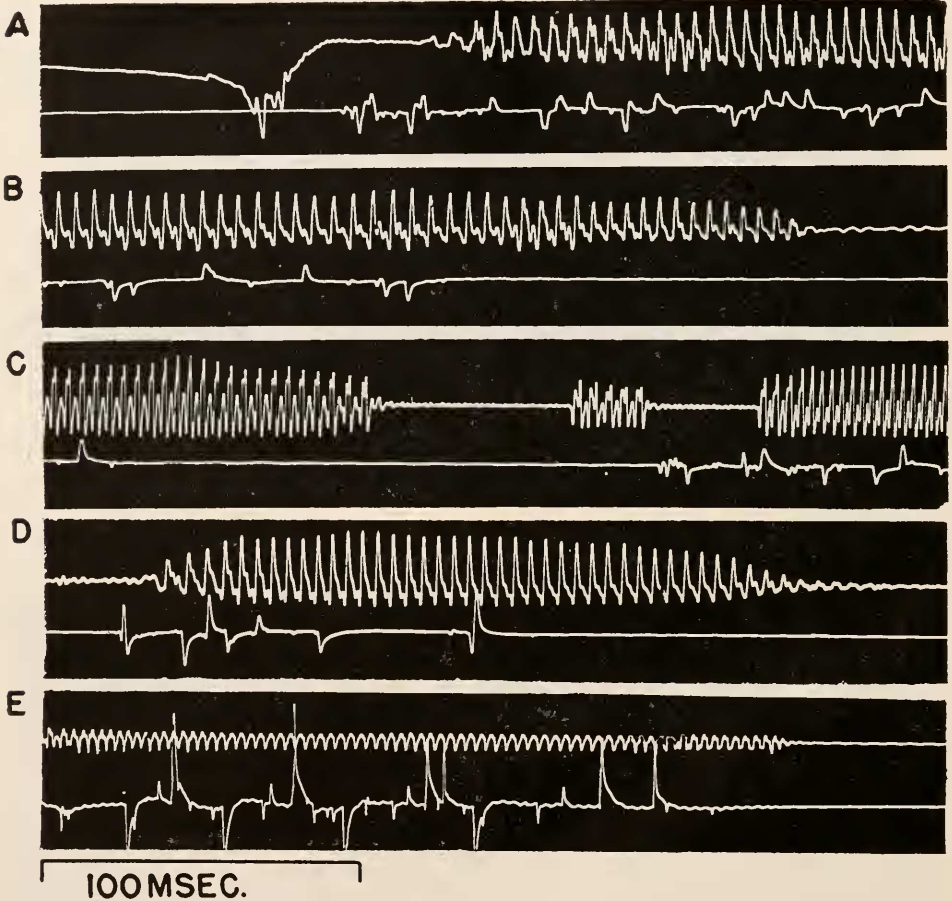


FIGURE 3. Spikes (lower trace) and thoracic movements (upper trace) in several flies. A. The onset of flight in *Calliphora*. B. Spontaneous termination of flight in the same insect. C. Irregular flight in the same insect following amputation of the wings. D. Short spontaneous (mid-air) burst of flight movements in *Eristalis*. E. Termination of flight in *Lucilia* after wing amputation. The spikes have been recorded with increased amplification to show the small sinusoidal potential.

spontaneously while suspended in mid-air. When this occurred (Fig. 3 B, D), the frequency of thoracic movement often remained unchanged while the amplitude declined steadily in stepless fashion, sometimes leaving a small trail of oscillation after the fly had apparently folded its wings. The smooth nature of the ampli-

tude change is particularly evident in the short flight of *Eristalis* (Fig. 3 D). Occasionally flight termination was quite abrupt (Fig. 3 C).

During the take-off, a series of spike potentials precede thoracic movements by 10 to 30 milliseconds (Fig. 3 A, D), and continue in an irregular fashion throughout the flight. Although at first the spike sequence appears to be random, once steady flight is established, a rough rhythm (Fig. 4) can be distinguished which has no phase-relation to the wingbeat. In long records it is possible to identify five or six sets of spikes, each set having its own sign, form, and repetition rate. In Figure 4 A and B, the downward spike shows constant form and size, and appears at regular intervals which differ from the intervals between similarly identifiable sets of spikes of opposite sign. Each set of spikes suggests activity of a single unit which is operating without synchronization with other units or with the sequence of muscular changes. In short or abortive flights (Fig. 3 D), a single short burst of spikes in several units may precede the peak of thoracic movement.

Each spike appears to have a duration of 5–10 milliseconds and a magnitude of 5 to 20 millivolts. In this respect, it is quite similar to the muscle potential recorded in *Periplaneta* (Roeder and Weiant, 1950). Increased amplification reveals in some (Figure 3 E) but not all records of thoracic potentials a low-voltage sinusoidal wave previously noted by Pringle (1949). This low-voltage wave follows the thoracic movements in frequency and amplitude, and may be an artifact due to the movement of electrically polarized muscle under the electrode pair. However, its origin is uncertain and it is discussed later.

Upon termination of the flight in mid-air (Fig. 3 B, D), thoracic movements continue for 20 to 40 cycles after cessation of the spike sequence. Although spikes were never detected when the fly had been motionless for some time, in one case (Fig. 3 C), following wing amputation an insect showed quite erratic bursts of activity. During one of these bursts movement ceased abruptly at the usual interval after the cessation of spike activity. One-tenth of a second later there was a short burst of five cycles of thoracic movement without the usual introductory spikes. After another pause spikes resumed followed by the return of steady flight.

Hymenoptera. Several specimens of the wasp, *Vespa*, were flown in a similar manner. Flight was steady and well sustained, and a regular sequence of thoracic movements and spikes bore, as in the flies, no phase relation with each other (Fig. 4 C). On the whole, the spikes in the wasp showed a more pronounced rhythm of their own, although the same mechanism appears to be operating in both flies and wasp. Several unsuccessful attempts were made to fly bees, but they showed a high mortality following insertion of the electrodes.

LOADING, WINGBEAT FREQUENCY, AND SPIKE FREQUENCY

From the incomplete survey reported above, it is apparent that the relatively low wingbeat frequency (20 to 40 per second) occurring in the roach and moth is associated with spikes recurring once during each wingbeat. On the other hand, the high wingbeat frequency (over 100 per second) recorded in the flies and wasp is associated with an asynchronous sequence of spikes at much lower frequency. In order to determine whether there is a basic difference in the mechanism of muscle excitation in these two groups, or whether the difference is only quantitative, de-

pending upon the wingbeat frequency, attempts were made to alter the loading of the wings.

The mass of air moved by the wing has a damping effect upon the wingbeat, reducing its frequency. This relation has been subjected to rigorous analysis by Chadwick and Williams (1949) for *Drosophila*, in which amputation of the wings or flight under reduced atmospheric pressure increases the wingbeat frequency as much as 100 per cent. Therefore, attempts were made to alter the wingbeat frequency of the insects mentioned above by amputation of the wings close to the thorax. This operation appeared to have little or no effect upon the ability of the insects to "fly" when attached to the stylus.

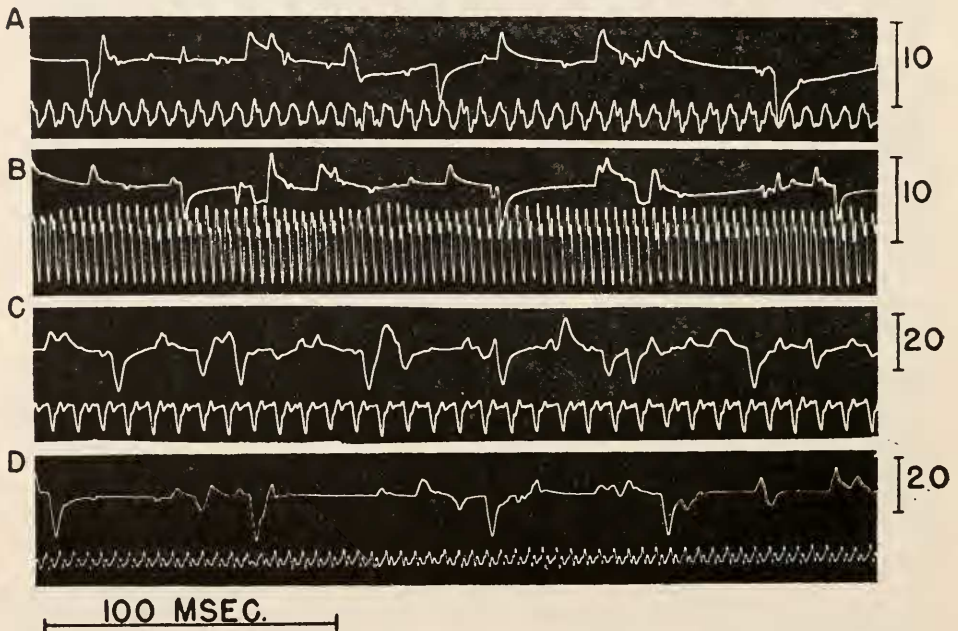


FIGURE 4. Spikes (upper trace) and thoracic movements (lower trace) during steady flight. A. *Lucilia*. B. The same after amputation of the wings. C. *Vespa*. D. The same insect after amputation of the wings. Vertical calibration, millivolts.

In the roach and moth (Fig. 2 B), close amputation of the wings appears to have little effect on the wingbeat frequency. In the latter insect there is a small but consistent decrease in frequency (Table I) although perfect synchrony between spikes and wing cycles is maintained. This suggests that the motor mechanism of the wings in these insects is driven by a central nervous pacemaker whose activity is more or less independent of the load. The slight but constant decrease in frequency in the moth could be due to the elimination of sensory endings of stimulatory function located on the wings.

In the flies (Figs. 3 C, 4 A and B) and wasp (Fig. 4 C and D), amputation of the wings produced the expected increase in the frequency of thoracic movement. While the frequency of thoracic movement almost doubled after this operation, the sequence of spikes recorded from the thoracic muscles either showed little change

or declined in frequency. Changes in wingbeat and in spike frequency following wing amputation are summarized in Table I. It will be noted that while the wingbeat spike quotient remains at unity in the roach and moth, it increases from a value of 4-18 when the wings are intact to 14-40 after wing amputation in the flies and wasp. The increase in w/s quotient is due both to an increase in wingbeat frequency and to a decrease in spike frequency following wing amputation.

TABLE I
*Frequency of thoracic vibration and potentials during flight **

Temp. °C.	Insect	With wings			Without wings		
		Wing rate/sec.	Spikes per sec.	Quot. W/S	Wing rate/sec.	Spikes per sec.	Quot. W/S
24	Periplaneta	28	28	1	33	33	1
22	Agrotis	30	30	1	26	26	1
24	Agrotis	41	41	1	39	39	1
		39	39	1	37	37	1
		42	42	1	40	40	1
24	Vespa	119	22	5	203	13	16
		112	29	4	201	14	14
25	Calliphora	138	11	13	186	8	22
		146	16	9	193	8	24
26	Lucilia	156	10	16	286	8	36
		140	8	18	285	7	41

* Measurement of spike frequency could be made only when this had become constant after several minutes of steady flight. This condition was not attained with all of the insects flown. Measurements were made to the nearest whole number.

Thus, the neuromuscular mechanism of the flies and wasp appears to be once more in contrast with that of the roach and moth. The increase in wingbeat frequency following reduction of the wing load might be considered to be due to a reduction in the natural period of the mechanically oscillating system envisaged by Pringle. On the other hand, the spike frequency in both groups shows either no change or a definite decrease following removal of the wings. This could be due either to a reduction in sensory input to the nerve centers regulating flight (due to elimination of sense organs on the wings), or in the case of the flies and wasp, to a central nervous mechanism regulated by negative feed-back from proprioceptors sensitive to the excursion of wing-base, thoracic sclerites, or indirect flight muscles.

ELECTRICAL STIMULATION OF THE FLIGHT MUSCLES

Indirect electrical stimulation of the muscles of the leg (Pringle, 1939), or of the exposed tergal remotor muscle (Roeder and Weiant, 1950) of the roach produces twitches always preceded by a muscle spike potential. In contrast, Pringle (1949) noted that the indirect flight muscles exposed by hemisection of the thorax

of a fly could not be excited by any form of electrical stimulus applied either to the ganglion or to the muscle surface, while the muscles of the legs and proboscis could readily be made to contract by electrical stimulation. This observation was confirmed on several genera of flies.

In the course of the observations reported above, many of the flies tested failed to fly upon removal of the platform, although they continued to move their legs. It is presumed that these failures were due to injury incurred upon insertion of the electrodes into the thorax. In several cases, electrical stimuli were delivered to these refractory flies via the electrodes normally used to record potential changes within the thorax. It was found that many of these insects could be made to "fly" continuously at their normal wingbeat frequency of over 100 per second, if stimulated with brief shocks at any frequency from 3 to 20 per second. This would occur only if the tarsi were out of contact with the platform. Stimulus frequencies less than 3 per second produced only a brief twitch of the wings, while frequencies higher than 20 per second produced no additional effect beyond flight movements at the normal flight frequency. One insect, a large specimen of *Tabanus*, could not be induced to fly even by this treatment. If the tarsi of this insect were in contact with the platform, stimulation produced a maximum extension of all legs. If the insect was suspended in mid-air, each stimulus produced a strongly damped oscillation of the thorax at approximately the natural wingbeat frequency.

These results may be compared with those of Heidermanns (1931), who stimulated the flight muscles of a dragonfly by means of electrodes inserted into the thorax. In this insect (which has a wingbeat frequency in the neighborhood of 30 per second) a wing movement followed each shock up to a frequency of 25-30 per second. At higher frequencies (45-50 per second) of stimulation, the muscles went into a tetanus.

DISCUSSION

In considering these experiments, it should be recognized that the flight performance of insects prevented from making forward progress must differ in many details from that occurring during free flight. One has only to watch the maneuvers of a free-flying insect to realize that its performance must depend upon a number of delicately balanced sensory feed-backs (Pringle, 1948; Weis-Fogh, 1950) and muscular adjustments. For instance, in performing the experiments described above, it was noted that flies would take off more readily and fly for longer periods if the platform under the tarsi were allowed to rotate freely so as to simulate forward locomotion before the take-off. Again, the flight reaction time of 40-60 milliseconds (Fig. 3 A) is both variable and long compared with that (21 milliseconds) determined by high-speed photography of the movements of a free fly when a bullet jerks away the platform upon which it is standing (Herget, 1950).

However, the experiments completely confirm the observation of Pringle (1949) of the lack of synchrony between spikes and wing movement in flies, and indicate that a similar state of affairs exists in wasps and possibly in other Hymenoptera. On the other hand, roaches and moths which have a low wingbeat frequency appear to have a more conventional mode of excitation of the flight muscles.

Excitation of the Flight Muscles in Diptera and Hymenoptera

According to Pringle, the situation in flies could be explained on the assumption that the arrival of a motor nerve impulse (signalled by a spike) "alters the state of the contractile elements in such a way that they become susceptible to the stimulus of stretching. On being stretched, the myofibrils respond with a twitch-like contraction whose duration is controlled by the loading, and then relax." Alternate twitches in vertical and horizontal indirect flight muscles would thus maintain in a state of oscillation at its natural period the mechanically resonant system consisting of the muscle tension, elastic characteristics of thorax, and wing load. The presence of a nervously conditioned, mechanically resonant system is confirmed by many of the observations made in this paper, namely: a) constancy of wing-beat frequency during amplitude changes at the onset and termination of flight; b) smooth changes in amplitude under the same conditions; c) inverse relation between spike frequency and wing beat frequency upon changes in loading; d) increase in wingbeat frequency upon reduction in loading; e) lack of excitability in flight muscles when the thorax is opened and the mechanical system presumably disturbed; and f) possibility of maintaining morphologically intact but moribund flies in flight at their normal frequency by electrical stimulation at any frequency.

Although Pringle's hypothesis provides an adequate explanation of the operation of the wings of flies during flight, it appears to provide no way in which the first contraction can be initiated if stretch is the immediate cause for contraction. On the other hand, the arrival of a motor impulse cannot be the immediate excitatory agent, since spikes may appear many milliseconds before signs of muscular activity (Fig. 3 A and D) and recur at no fixed point during the cycle of wing movement. Therefore, the following concept is presented as an elaboration of Pringle's original theory. In order to bring the indirect flight muscles of flies to a point where they drive the resonant system outlined above, two factors are necessary. One factor is the resting tension of the muscles, which depends upon their attachment to the inner surface of the semi-rigid, roughly spherical thorax. The tension is presumably constant in a resting fly, but is substantially reduced by any operation which interferes with the mechanical continuity of the thorax, such as hemisection. The second factor will be termed the neural factor, since it depends upon the arrival of motor impulses. It is presumably low or absent in the resting intact fly but is built up in a series of increments and maintained by the arrival of nerve impulses as indicated by the recorded spikes. The build-up of the neural factor superimposed upon the pre-existing tension factor steadily raises the muscle excitability until a twitch occurs in one set of muscles. The twitch causes a sudden increase in the tension of the antagonistic group of muscles which have been brought to some point just short of threshold by impulses in another nerve fiber. This increment in tension carries them over threshold so that they shorten and increase the tension in the other group. At this point, the myogenic mechanically resonant system of Pringle takes over, the oscillation continuing so long as the injection of occasional impulses maintains the neural factor at a level sufficient to offset the damping effects of the load.

It must be supposed that both factors must reach a certain level before muscular activity commences. In the resting or moribund fly, the tension factor is present but the neural factor is so low that no activity occurs. In the hemisected

thorax, electrical stimulation may raise the neural factor, but the tension factor is reduced so that again no contraction occurs. The time course of the neural factor can only be approximated, since it is not accompanied by an electrical sign. It appears to accumulate and dissipate at a much slower rate than the time course of individual spikes, since the latter may precede muscular movement by 5–30 milliseconds at the onset of flight, and cease an even longer time before cessation of movement at flight termination. In a very brief flight the burst of spikes may be terminated even before thoracic movements reach their full amplitude. In some records, periodic increases in amplitude of thoracic movements appear to bear some relation to increase in the spike frequency. Thus, the change produced by the spikes develops and dissipates relatively slowly compared with the electrical time course of a spike, and the latter have a cumulative action in bringing about its development. Since five or six sets of spikes in the same record are independent of each other in frequency, the rate of accumulation and dissipation of the neural factor must vary in different motor units.

The importance of tension as a factor in the excitation and contractility of smooth muscle is widely recognized. Sudden distension of the ureter may cause either a single, or an oscillatory contraction of its wall (Bozler, 1947). In this case, the tension-initiated contraction is accompanied by a potential change which is not evident during contraction of the indirect flight muscles of flies, although the small oscillatory potential (Fig. 3 E) which follows the thoracic movements remains unaccounted for. Direct studies of the effects of applied tension on the excitability of insect flight muscle have yet to be made.

Types of Flight Muscle Excitation Compared

Since there is no information regarding the relation between spike and wing-beat frequency in insects belonging to other orders, one can only speculate upon the significance of the difference between roach and moth on one hand, and flies and wasp on the other. Perhaps the mechanical characteristics of the thorax of the flies and wasp favor a degree of muscle tension which makes this the dominant factor in muscle excitation after the system has been 'cranked up' by the neural factor. The system then operates at its natural period of vibration. By the same token, the less compact thorax and larger wing area of the roach and moth may not provide the requisite muscle tension and resonance necessary for myogenic oscillation; hence, the dominant factor in causing muscle excitation is the arrival of a motor nerve impulse.

A transition is suggested by the observations of Boettiger and Furshpan (1950 and personal communication). They consider the energy of the contracting flight muscles to be stored in a mechanical stop (click mechanism) which, when overcome by increasing muscle tension, causes an abrupt movement of the wings. Boettiger recorded potentials and movements in several flies, including a crane fly. This slow-flying, large-winged fly had a wingbeat frequency of 36 per second and a sequence of spikes which showed a general 1:1 relation with the cycle of wing movement. However, the spikes and wing movements were not locked precisely in phase as in the roach and moth. Amputation of the wings of the crane fly increased the frequency of thoracic movement to 90 per second, while the spike frequency was unchanged. Thus, the difference observed in the two groups of insects

may depend solely upon the physical characteristics of the system. Voskresenskaya (1947) recorded the response of the flight muscles of a locust when the ganglion was stimulated at various frequencies up to 100 per second. She noted a tendency of the muscles to contract at 18 per second and a sequence of flight movements after stimulation had ceased. Since this after-effect was blocked by nicotine, it was apparently due to a central ganglionic after-discharge, and not a myogenic oscillation similar to that observed in flies.

The data summarized in Table I also suggest a compromise between the two types of neuromuscular mechanism. Although wing amputation brings about an increase in wingbeat frequency in the flies and wasp, and either little or no change or a decrease in the roach and moth, this operation affects the spike frequency in the same way in both groups of insects. This suggests that during flight the motor output of the central nervous system of both groups depends in part either upon a sensory inflow from mechanoreceptors on the wings, or upon negative feed-back from receptors sensitive to the rate of deformation of the moving parts of the thorax, flight muscles or wingbase. The halteres of flies (Pringle, 1948) and hair plates on the head capsule of locust (Weis-Fogh, 1950) have been shown to regulate orientation during flight (see also Waterman, 1950), and may, together with the proprioceptors mentioned above, form part of the general sensory field which maintains the output of motor impulses to the flight muscles. Therefore, the neural component of the flight mechanism appears to be similar in both groups of insects, and the difference between them may lie merely in the greater importance of resting tension as an excitatory factor of the flight muscle in flies.

SUMMARY

1. Simultaneous records were made of thoracic movements and potential changes within the thorax of a number of insects during stationary flight.
2. The American roach and a moth with a wingbeat frequency in the range 20–40 per second showed complete synchrony between spikes and movements, and little change or a decrease in the frequency of both phenomena when the wings were amputated.
3. Several flies and a wasp with a wingbeat frequency above 100 per second showed no synchrony between spikes and movements, the former appearing once in every 5–20 wingbeats. Amputation caused either little change or a decrease in spike frequency, while the wingbeat frequency increased by nearly 100 per cent.
4. While the muscles of the former group retain their excitability to indirect electrical stimulation after dissection, the flight muscles of the latter are inexcitable following hemisection of the thorax. However, if the thorax is intact the indirect flight muscles of flies can be driven at the natural flight frequency by any stimulus frequency above 3 per second.
5. It is concluded that in the flies and wasp, the level of resting tension determines a degree of excitability in the flight muscles. This excitability is augmented by the accumulation of a neural factor brought about by the arrival of motor nerve impulses (spikes). Upon threshold being reached in one set of indirect flight muscles, they contract, and by increasing the tension factor in the antagonists, bring them rapidly to threshold. Flight continues as a myogenic oscillation at a natural frequency determined by muscle tension, elasticity of thorax,

and wing load, provided the neural factor is maintained at a certain level to offset damping.

6. In the roach and moth, the resting tension does not appear to be sufficient to give the system resonance or to contribute greatly to the muscle excitability. Therefore, the arrival of a motor impulse is the determining factor in contraction of the flight muscles.

LITERATURE CITED

- BOETTIGER, E. G., AND E. FURSHIPAN, 1950. Observations on the flight motor in Diptera. *Biol. Bull.*, **99**: 346-347.
- BOZLER, E., 1947. The response of smooth muscle to stretch. *Amer. J. Physiol.*, **149**: 299-301.
- CHADWICK, L. E., 1947. The respiratory quotient of *Drosophila* in flight. *Biol. Bull.*, **93**: 229-239.
- CHADWICK, L. E., AND C. M. WILLIAMS, 1949. The effects of atmospheric pressure and composition on the flight of *Drosophila*. *Biol. Bull.*, **97**: 115-137.
- HEIDERMANNS, C., 1931. Reizphysiologische Untersuchungen an der Flugmuskulatur von *Aeschna coerulea*. *Zool. Jahrb., Abt. Physiol.*, **50**: 1-31.
- HERGET, C. M., 1950. Reaction time of the common housefly (*Musca domestica*). *Science*, **112**: 62.
- PRINGLE, J. W. S., 1939. The motor mechanism of the insect leg. *J. Exp. Biol.*, **16**: 220-231.
- PRINGLE, J. W. S., 1948. The gyroscopic mechanism of the halteres of Diptera. *Phil. Trans. Roy. Soc. London*, **233**: 347-384.
- PRINGLE, J. W. S., 1949. The excitation and contraction of the flight muscles of insects. *J. Physiol.*, **108**: 226-232.
- ROEDER, K. D., AND E. A. WEIANT, 1950. The electrical and mechanical events of neuromuscular transmission in the cockroach, *Periplaneta americana*. *J. Exp. Biol.*, **27**: 1-13.
- SOTAVALTA, O., 1947. The flight tone (wing-stroke frequency) of insects. *Acta Ent. Fennica*, **4**: 1-117.
- VOSKRESENSKAYA, A. K., 1947. Functional peculiarities of the neuro-muscular apparatus of the wings of insects. *J. Physiol. U.S.S.R.*, **33**: 381-392.
- WATERMAN, T. H., 1950. Flight instruments in insects. *Amer. Scientist*, **38**: 222-238.
- WEIS-FOGH, T., 1950. An aerodynamic sense organ in locusts. *Proc. VIII Intern. Congr. Entomol.*, 1-5.
- WIGGLESWORTH, V. B., 1949. The utilization of reserve substances in *Drosophila* during flight. *J. Exp. Biol.*, **26**: 150-163.
- WILLIAMS, C. M., L. A. BARNES, AND W. H. SAWYER, 1943. The utilization of glycogen by flies during flight and some aspects of the physiological ageing of *Drosophila*. *Biol. Bull.*, **84**: 263-272.
- WILLIAMS, C. M., AND R. GALAMBOS, 1950. Oscilloscopic and stroboscopic analysis of the flight sounds of *Drosophila*. *Biol. Bull.*, **99**: 300-307.